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Citation for published version:

Fikse, WF & Banos, G 2001, 'Weighting factors of sire daughter information in international genetic evaluations', *Journal of Dairy Science*, vol. 84, no. 7, pp. 1759-1767. [https://doi.org/10.3168/jds.S0022-0302\(01\)74611-5](https://doi.org/10.3168/jds.S0022-0302(01)74611-5)

Digital Object Identifier (DOI):

[10.3168/jds.S0022-0302\(01\)74611-5](https://doi.org/10.3168/jds.S0022-0302(01)74611-5)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

Published In:

Journal of Dairy Science

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Weighting Factors of Sire Daughter Information in International Genetic Evaluations

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ABSTRACT

International genetic evaluations of dairy bulls are currently based on national genetic evaluation results. Total number of daughters in a country is used to weight national information, but may not optimally reflect the precision of a sire's daughter contribution to international genetic evaluations. This study investigates the impact of alternative weighting factors on international evaluation results. A conventional progeny test scheme was simulated for two dairy cattle populations, with semen exchange at a fixed rate after each generation. True breeding values for both populations were generated as bivariate normal deviates. Each cow had three lactation records in one country only. After 10 generations of selection, all records were used in national breeding value prediction. National breeding values of bulls were used as input to international evaluations. Seven different weighting factors were evaluated: 1) total number of daughters; 2) total number of lactations; 3) as (one) also adjusted for finite contemporary group size; 4) as (three) also adjusted for distribution of daughters over contemporary groups; 5) effective daughter contribution considering finite contemporary group size and correlation between repeated records; 6) as (five) also considering the reliability of the daughter dam evaluation; and 7) as (five) also considering the reliability of the daughter female ancestors' evaluations. Using the last two weighting factors yielded empirically unbiased estimates of sire variance. Using total number of daughters overestimated genetic variance by up to 7%. In general, international breeding values were marginally affected by choice of weighting factor. The effect was larger when different national evaluation models had been applied in the two countries. International reliabilities for the last two weighting factors were close to expectation, whereas

using total number of daughters resulted in 1 to 4% negative bias. In practice, different countries apply a wide range of national evaluation models, and genetic ties may be weak between some populations, thereby increasing the potential effect of weighting factors on international comparisons. The weighting factor developed in this study, which considers contemporary group structure, correlation between repeated records, and reliability of dams of daughters, should replace total number of daughters in international genetic evaluations of dairy sires.

(Key words: daughter information, international comparisons, weighting factor, simulation)

Abbreviation key: CG = contemporary group; MACE = multiple-trait across country evaluation; ML = national evaluation based on three lactations (no culling); MLcull = national evaluation based on three lactations (culling); MSEP = mean squared error of prediction; PEV = prediction error variance; SL = national evaluation based on first lactation records.

INTRODUCTION

National genetic evaluation results can be combined in a multiple-trait sire model to provide international genetic comparisons (Schaeffer, 1994). The method currently used is known as multiple-trait across country evaluation (MACE). The dependent variable for the international sire model is preferably an unregressed measure of progeny performance, free of any systematic effects other than the bull's genetic value. De-regressed national breeding values and daughter yield deviations can be applied in this context (Sigurdsson and Banos, 1995).

Precision of daughter information expressed either as de-regressed national breeding value or as daughter yield deviation, varies for each bull both within and across country. This variability needs to be accounted for in international comparisons and can be directly accommodated in the residual (co)variance structure of the international sire model. However, this would require the inverse of the coefficient matrix of the mixed

Received September 20, 2000.

Accepted January 17, 2001.

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model equations from each country. Calculating the inverse is computationally prohibitive. Therefore, development of alternative factors to weight a sire's daughter information in international evaluations is desirable.

Sources of variation in precision of daughter information include number of daughters that are considered in the national evaluation, number of lactations of each daughter, whether or not lactations were in progress or prematurely terminated, daughter dam information, and contemporary group (CG) structure. Because no other uniformly defined figure describing precision of daughter information has been available, total number of daughters of each bull is currently being used as weighting factor in routine international genetic evaluations of dairy sires (Banos and Sigurdsson, 1996). This figure may not, however, be the most representative of precision of daughter information because it ignores most of the above-mentioned factors that cause precision of daughter information to vary between bulls.

In a study with data from two countries, Fikse and Banos (1997) considered effective number of daughters derived from national reliabilities as weighting factor. Genetic parameters and international breeding values were minimally influenced. However, international reliabilities were affected. Nearly perfect national reliabilities do not distinguish among bulls with very large numbers of effective daughters. Also, national reliabilities include information from relatives other than sire daughters causing double counting when the numerator relationship matrix is included in international evaluation. These factors were not accounted for in the study of Fikse and Banos (1997).

The objectives of this study were to develop new weighting factors associated with daughter information for application in MACE and to investigate the impact of these weighting factors on international genetic evaluations of dairy bulls.

MATERIALS AND METHODS

Two dairy cattle populations practicing selection were simulated for 10 generations. Phenotypic data were then used for within-population (national) breeding value prediction. National breeding values were used as input into international genetic evaluations. Seven weighting factors were developed and evaluated.

Simulation of Data

A conventional progeny test scheme was simulated in two equal-sized populations. The simulation comprised 10 generations, with 36,000 cows and 300 progeny test bulls per generation in each population. In

every generation, 10 sires and 150 dams were selected as parents of young bulls. An additional 30 bulls were selected based on progeny test results to be used as proven bulls in the next generation. Progeny group size for young bulls was normally distributed with a mean of 80 and a standard deviation of five. Proven bulls had 400 additional daughters in the following generation.

In each generation, parents to produce the next generation were selected on within-population predicted breeding values. Mating was random and resulted in one offspring for each mating that produced female calves. Two full brothers were generated from each mating that produced male calves, allowing for progeny tested full sib families. From generation four onwards, sires of sons and sires of cows were exchanged between populations at a fixed rate of 50% to ensure sufficient genetic links between populations. Exchange sires were randomly taken from the within country selected sires.

True breeding values were simulated as: $TBV_{anim} = 0.5 TBV_{sire} + 0.5 TBV_{dam} + \Phi_{anim}$, where TBV_{sire} and TBV_{dam} are true breeding values for the sire and dam, respectively, and Φ_{anim} represents the Mendelian sampling term. This term was sampled from a pseudo normal distribution with mean zero and standard deviation $0.5 \cdot \sigma_a \cdot \sqrt{1 - (F_{sire} + F_{dam})/2}$, where σ_a is the genetic

standard deviation, and F_{sire} and F_{dam} are the inbreeding coefficients of the sire and dam, respectively. Genetic variance and heritability were assumed to be 100 and 0.30, respectively. The genetic correlation between populations was 0.90, reflecting possible differences in animal performance in different environments (genotype by environment interaction).

Phenotypic records for cows were generated as: $y = CG + TBV_{anim} + \text{residual}$, where CG is the contemporary group effect. For each cow, three lactation records were simulated as repeated observations with repeatability equal to 0.50. All records of a cow were simulated in the generation of birth. Contemporary group size was normally distributed with mean values of 10 and 20, a coefficient of variation of 5% and a minimum size of five. Contemporary group effects were generated using a normally distributed random deviate with mean and standard deviation equal to zero and 15, respectively.

Breeding value prediction for within-generation selection was based on first-lactation records only. The model included fixed contemporary groups and genetic groups for missing parents defined according to generation and population of origin, and a random animal effect. Simulated genetic and residual variances were used. The mixed model equations were set up and solved following the method of implicit representation (Tier and Graser, 1991). Gauss-Seidel iteration was applied, with exponential extrapolation (Misztal et al.,

1987) every 50th round. Breeding values were assumed converged when the average relative difference between consecutive rounds was smaller than 10^{-6} . Fifteen replicates of each scenario were carried out.

National Breeding Value Prediction

At the end of the last generation, three sets of breeding values were predicted for all animals within each population to be used as input into the international genetic evaluation (Table 1). Firstly, only first-lactation records were used, and the model included fixed contemporary group and phantom parent group effects and a random animal effect (**SL** model). Secondly, records on all three lactations were used by applying the same model as before except extended with a permanent environmental effect (**ML** model). Lastly, three lactations were considered in the evaluation, but culling on phenotypic records had been practiced prior to the breeding value prediction (**MLcull** model). The culling process was simulated by deleting certain portions of the second- and third-lactation records; 70% of the cows were allowed to have second- and 50% third-lactation records.

International Breeding Value Prediction

International genetic evaluations were calculated with a multiple-trait sire model also known as MACE (Schaeffer, 1994):

$$y_i = \mu_i \mathbf{1} + \mathbf{Z}_i \mathbf{Q} \mathbf{g}_i + \mathbf{Z}_i \mathbf{s}_i + \mathbf{e}_i,$$

where μ_i is the mean for country i , \mathbf{g}_i the genetic group effect and \mathbf{s}_i the random sire effect for country i , \mathbf{Z}_i the matrix that relates observation to sires, and \mathbf{Q}_i the matrix that relates sires to genetic groups. Dependent variable \mathbf{y}_i were de-regressed national breeding values of bulls (Sigurdsson and Banos, 1995) obtained using a model with the same systematic effects subsequently included in the international sire model (Jairath et al., 1998). $\mathbf{V}(\mathbf{s}) = \mathbf{A} \otimes \mathbf{G}_0$, where \mathbf{A} is the additive genetic relationship matrix, \mathbf{G}_0 a matrix with sire (co)variances between traits measured in the two populations, and \otimes the Kronecker product. The relationship matrix was based on sire and maternal grandsire. Maternal grand-

dams were treated as unknown and included in the genetic group definition. Unknown parents, including maternal granddams and ancestors of imported bulls in within country de-regression and sire variance estimation, were grouped according to generation, population of origin, and path of selection. Genetic groups were treated as random by adding the inverse of \mathbf{G}_0 to the diagonal of the genetic group equations. The assumed (co)variance structure for the residuals was: $\mathbf{V}(\mathbf{e}) = \sum_i \mathbf{D}_i \sigma_{e_i}^2$, where \mathbf{D}_i is a diagonal matrix with weighting factors as elements.

Sire variances were estimated within each population using an EM-REML procedure (Sigurdsson et al., 1996). International breeding values were calculated using estimated sire variances and simulated genetic correlations. MACE mixed model equations were solved with iteration on data and iteration was finished when the average relative difference between solutions from consecutive rounds was less than 10^{-8} for all traits. Harris and Johnson's (1998) approximation method was used to compute international reliabilities.

Weighting Factors

Seven different weighting factors were developed:

1. Total number of daughters, w_{1_i} of sire i ; this is the weighting factor currently used in routine international genetic evaluations.
2. Total number of lactations, w_{2_i} of daughters of sire i .
3. Number of first lactations adjusted for CG size, computed as follows:

$$w_{3_i} = w_{1_i} - \sum_k \frac{1}{n_{jk}},$$

where n_{jk} is the size of CG j in which daughter k of sire i made her first lactation, and summation is over all daughters of sire i .

4. Number of first lactations adjusted for CG size and distribution of daughters over CG, computed as:

$$w_{4_i} = w_{1_i} - \sum_j \frac{n_{ij}^2}{n_j},$$

where n_{ij} is the number of daughters of sire i in CG j , n_j is the size of CG j , and summation is over

Table 1. Within population breeding value prediction models.

Model	Effects ¹	Trait	Culling
Single lactation	CG + genetic group + animal + residual	First lactation	No
Multiple lactation	CG + genetic group + PE + animal + residual	All lactations	No
Multiple lactation	CG + genetic group + PE + animal + residual	All lactations	Yes

¹CG = Contemporary group; PE = permanent environment.

all CG where sire *i* has daughters; this is the exact effective number of daughters for a single-trait single-lactation sire model.

5. Effective daughter contribution, computed as:

$$w_{5_i} = \sum_k \frac{\lambda R_k(o)}{4 - R_k(o)},$$

where summation is over all daughters of sire *i*, $\lambda = (4 - h^2)/h^2$, and $R_k(o)$ is the reliability of animal *k*'s own record, computed as:

$$R_k(o) = \frac{n_k \cdot h^2}{1 + (n_k - 1) \cdot r},$$

where *r* is the repeatability of an animal's records, and n_k is the number of lactations of daughter *k* of sire *i* adjusted for CG size, computed as:

$$n_k = \sum_l 1 - \frac{1}{n_{jkl}},$$

where n_{jkl} is the size of CG *j* in which daughter *k* of sire *i* made her *l*th lactation; this figure reflects the contribution of animal information to the parent (VanRaden and Wiggans, 1991).

6. Effective daughter contribution, including performance of the dam of daughter *k*:

$$w_{6_i} = \sum_k \frac{\lambda R_k(o)}{4 - R_k(o) \cdot (1 + R_{dam}(o))},$$

where $R_{dam}(o)$ is the reliability of the dam's own performance, and summation is over all daughters of sire *i*.

7. As in 6, but $R_{dam}(o+p)$ was used instead of $R_{dam}(o)$, thus considering records from all female ancestors of the daughter:

$$R_{dam}(o+p) = \frac{R_{dam}(o) + R_{dam}(p) - 2R_{dam}(o)R_{dam}(p)}{1 - R_{dam}(o)R_{dam}(p)},$$

where:

$$R_{dam}(p) = .25 \cdot R_{granddam}(o+p);$$

computation of this weighting factor requires the data file to be processed from oldest to youngest animals.

Weighting factors 1 and 3 to 7 were computed when national genetic evaluations were based on first-lactation records only. Weighting factors 1, 2, and 5 to 7 were computed when national genetic evaluations were based on multiple lactation records.

RESULTS AND DISCUSSION

Table 2 shows the average value of each weighting factor. The average daughter group size (w_1) for bulls was approximately 115. Number of lactations (w_2) was approximately 346 when three lactations per cow were considered, and about 25% lower in presence of culling. Accounting for fixed effects (w_3 and w_4) reduced the contribution by 10 and 6% for CG size of 10 and 20, respectively (SL model). Considering female ancestors of daughters (w_6 and w_7) increased the relative amount of daughter contribution in all cases, having the largest effect on large CG sizes and national evaluations based on multiple lactations.

Genetic Parameters

Using total number of daughters (w_1) as weighting factor always overestimated sire variance (Table 3). When only first-lactation records were used in the national evaluation, bias in sire variance increased with

Table 2. Average¹ values for weighting factors for the three national evaluation models.

Weighting factor ²	Single lactation		Multiple lactation		Multiple lactation, culling	
	10 ³	20	10	20	10	20
w_1	115	115	115	115	115	115
w_2			346	346	254	254
w_3	103	108				
w_4	104	110				
w_5	102	109	183	187	153	158
w_6	117	124	201	205	171	175
w_7	119	126	203	206	172	177

¹Mean of 15 replicates; SE < 0.001.

² w_1 = Total number of daughters; w_2 = total number of lactations; w_3 = number of first lactations adjusted for finite contemporary group size; w_4 = number of first lactations adjusted for finite contemporary group size and daughter distribution; w_5 = effective daughter contribution; w_6 = w_5 plus the additional accuracy from records of the dam of the bull daughter; w_7 = w_5 plus the additional accuracy from records of all female ancestors of the bull daughter.

³Average contemporary group size.

Table 3. Relative bias¹ in estimated sire variance for seven weighting factors and three different national evaluation models.

Weighting factor ²	Single lactation		Multiple lactation		Multiple lactation, culling	
	10 ³	20	10	20	10	20
w ₁	1.65	2.13	7.66	7.98	5.25	6.03
w ₂			-4.65	-4.39	-4.39	-3.70
w ₃	3.54	3.03				
w ₄	3.63	3.11				
w ₅	3.87	3.19	0.88	0.96	0.98	1.30
w ₆	1.44	0.95	-0.16	0.06	-0.43	-0.05
w ₇	1.15	0.68	-0.24	-0.14	-0.57	-0.18

¹Relative bias computed by the difference between estimated and true sire variance as percentage of the true variance. Mean value of 15 replicates; SE < 0.06.

²w₁ = Total number of daughters; w₂ = total number of lactations; w₃ = number of first lactations adjusted for finite contemporary group size; w₄ = number of first lactations adjusted for finite contemporary group size and daughter distribution; w₅ = effective daughter contribution; w₆ = w₅ plus the additional accuracy from records of the dam of the bull daughter; w₇ = w₅ plus the additional accuracy from records of all female ancestors of the bull daughter.

³Average contemporary group size.

adjustment for CG structure (w₃ and w₄). Considering precision of mate information in the weighting factors (w₆ and w₇) decreased bias. Using total number of daughters severely overestimated sire variance when all three lactations were considered. Sire variances were underestimated with number of lactations as weighting factor but were nearly unbiased when CG structure, correlation between observations, and precision of mate information were considered (w₆ and w₇). Bias of sire variance tended to be larger with small CG (Table 3).

Observed biases may have resulted from an incorrect assessment of the precision of the predicted national breeding values that were input into MACE. Sire variance estimates are based on an EM-REML equation including two contributions: 1) a quadratic form of breeding values and the inverse of the relationship matrix, and 2) the trace of a matrix that is related to prediction error variance (PEV) of breeding values. Weighting factors only influence the second contribution; the first contribution is unaffected by weighting factors because national breeding values (rather than phenotypic observations) are used as input. If the weighting factor incorrectly assesses the amount of information on which breeding values are based, the second contribution is incorrect, thus introducing bias in the sire variance estimate. Considering CG structure and daughter distribution and ignoring correlations between observations on the same daughters leads to lower values for weighting factors, overestimates PEV of breeding values, and yields higher estimates of sire variances. Incorporating precision of mate information results in larger weights and lower estimates of sire variances. Only the last two weighting factors account

for all of these potential biases and, therefore, are expected to yield results that are not biased by these sources.

International Breeding Values

In general, weighting factors had small effects on international breeding values. Mean square error of prediction (MSEP), computed as the average squared difference between true and predicted breeding value, was nearly identical for all weighting factors for bulls with a national evaluation in one population only (Table 4). Choice of weighting factor had a larger impact when one population used SL and the other ML in national evaluation with total number of daughters less desirable than the other weighting factors (Table 4). For bulls with national evaluations in both populations, choice of weighting factor had practically no impact on international breeding values (results not shown).

The small impact of weighting factor choice on international breeding values is also demonstrated in Table 5. The maximum difference between international breeding values based on total number of daughters (current practice) and international breeding values based on other weighting factors for last generation bulls ranged from 0.09 to 0.18% of the genetic standard on the population of origin scale deviation. Differences on the other population scale were between 0.29 and 0.69% of the genetic standard deviation. Although figures from Table 5 pertain to ML, results for SL and MLcull were very similar.

Decomposing the MACE equation for individual bulls may help explain why only minor changes in international breeding values were detected. For bulls with a

Table 4. Mean square error¹ of prediction for international breeding values on local and foreign scale for bulls with a national evaluation in one population only.

Weighting factor ²	10 ³		20	
	ML in both countries ⁴	SL in one, ML in the other country	ML in both countries	SL in one, ML in the other country
w ₁	25.5	27.8	24.7	26.7
w ₅	25.5	27.7	24.7	26.5
w ₆	25.5	27.6	24.7	26.4
w ₇	25.5	27.6	24.7	26.4

¹Mean value of 15 replicates; SE < 0.2.²w₁ = Total number of daughters; w₅ = effective daughter contribution; w₆ = w₅ plus the additional accuracy from records of the dam of the bull daughter; w₇ = w₅ plus the additional accuracy from records of all female ancestors of the bull daughter.³Average contemporary group size.⁴National genetic evaluation systems in the two countries; ML = National evaluation based on three lactations (no culling); SL = national evaluation based on first lactation records.

national evaluation in one population only, the MACE equation can be written as follows (Klei et al., 1999; Mrode and Swanson, 1999):

$$IBV_{IMP} = PI_{IMP} + b \times (IBV_{EXP} - PI_{EXP}),$$

where PI, IBV, and b denote pedigree index, international breeding value, and theoretical slope of the conversion equation, respectively. The subscripts IMP and EXP indicate the importing and exporting country, respectively. The theoretical value for the slope of the conversion equation is $r_G \times \sigma_{s,IMP} / \sigma_{s,EXP}$, where r_G is the genetic correlation between countries and $\sigma_{s,IMP}$ and $\sigma_{s,EXP}$ are the sire standard deviations in the importing and exporting countries, respectively. The slope is expected to be the same when both populations apply the same national genetic evaluation models because any over- or underestimation of the sire variance in the two populations cancels out (Table 3). When countries apply different national genetic evaluation procedures, how-

ever, the slope of the conversion equation will be affected by choice of weighting factor. For the situations studied, the slope did not change significantly and, because no additional international information contributes to the Mendelian sampling term on the local scale ($IBV_{EXP} - PI_{EXP}$), IBV_{IMP} for these bulls would only be affected by changes in PI_{IMP} . Both populations in this study were well connected, therefore, PI_{IMP} was largely based on information from the importing population. Consequently, MACE did not add much extra information from the bull's country of origin to the pedigree index.

International Reliabilities

In general, international reliabilities on both local and foreign scale were underestimated when total number of daughters was used as the weighting factor (Table 6). Expected values were based on observed PEV for bull evaluations. Reliabilities based on total number of

Table 5. Maximum absolute difference in percentage of genetic SD units¹ between national breeding values based on total number of daughters and other weighting factors expressed on local and foreign scales. Results are from bulls of the last generation and national evaluations were based on three lactations.

Weighting factor ²	10 ³		20	
	Local	Foreign	Local	Foreign
w ₁
w ₂	0.18	0.69	0.16	0.65
w ₅	0.10	0.30	0.09	0.29
w ₆	0.11	0.36	0.11	0.35
w ₇	0.12	0.37	0.11	0.36

¹Mean value of 15 replicates; SE < 0.003.²w₁ = Total number of daughters; w₂ = total number of lactations; w₅ = effective daughter contribution; w₆ = w₅ plus the additional accuracy from records of the dam of the bull daughter; w₇ = w₅ plus the additional accuracy from records of all female ancestors of the bull daughter.³Average contemporary group size.

Table 6. International reliabilities¹ on the local and foreign scale for bulls with a national evaluation in one population only.

Weighting factor ²	Single lactation				Multiple lactation				Multiple lactation, culling			
	Local		Foreign		Local		Foreign		Local		Foreign	
	10 ³	20	10	20	10	20	10	20	10	20	10	20
w ₁	88	88	74	74	88	88	74	74	88	88	74	74
w ₂					95	95	79	79	94	94	78	78
w ₃	87	88	73	73								
w ₄	87	88	73	73								
w ₅	87	87	73	74	92	92	77	77	91	91	75	76
w ₆	88	89	74	74	93	93	77	77	91	92	76	76
w ₇	88	89	74	74	93	93	77	77	91	92	76	76
Expected ⁴	88	89	73	73	92	92	76	76	91	91	75	75

¹Mean of 15 replicates; SE < 0.002.²w₁ = Total number of daughters; w₂ = total number of lactations; w₃ = number of first lactations adjusted for finite contemporary group size; w₄ = number of first lactation adjusted for finite contemporary group size and daughter distribution; w₅ = effective daughter contribution; w₆ = w₅ plus the additional accuracy from records of the dam of the bull daughter; w₇ = w₅ plus the additional accuracy from records of all female ancestors of the bull daughter.³Average contemporary group size.⁴Expectation based on the observed prediction error variance.

daughters were identical across levels of information included in the national breeding value prediction. Using number of lactations as the weighting factor overestimated international reliability on both the local and foreign scale. Using weighting factors w₆ and w₇ yielded international reliabilities closest to their expectation. Such estimates on the local scale were also closer to the reliability of national breeding values computed with Meyer's (1987) approximation method (results not shown). Differences between weighting factors were less pronounced when SL or MLcull had been used in national evaluations because the magnitude of weighting factor differences was smaller for SL and MLcull than ML (Table 2). Patterns found for bulls with national evaluations in both populations were similar to those for bulls with one national evaluation only, although differences were not as large (results not shown). This is probably related to the higher reliabilities of bulls progeny tested in both populations.

Observed errors in international reliabilities were consistent with errors in the assumed precision of daughter information using the various weighting factors, i.e., if the weighting factor over(under)estimated the precision of daughter information, then the international reliability was over(under)estimated. Since true heritabilities and genetic correlations were used in this study, weighting factors were the only parameters that varied. When weighting factors over- or underestimated the precision of daughter information, international reliabilities were directly affected.

International reliabilities on the foreign scale were lower than on the local scale because less than unity

genetic correlations put less weight on foreign information. Foreign reliability would have been r_G^2 times the reliability on the local scale if neither daughter nor ancestor of the bull were available in the foreign population. Foreign reliability was on average two percent higher than r_G^2 times the reliability on the local scale (Table 6) since populations were well connected and many ancestors had daughters in both populations.

General Discussion

Results from this simulation study suggest that using total number of daughters as the weighting factor in international genetic comparisons introduces errors, especially when multiple records on animals are used in the national evaluation. Sire variance estimates and reliabilities of international breeding values appeared to be affected most.

Simulated genetic correlations were used in this international genetic comparison. Correlation estimates between countries using the various weighting factors were also obtained with the EM-REML procedure of Sigurdsson et al. (1996). When populations had applied similar national genetic evaluation procedures, estimated genetic correlations were unaffected by choice of weighting factor. Simulated correlations were used throughout this study to minimize sampling variation due to estimation of genetic correlations.

The optimal weighting factor should consider the effects of contemporary group structure, the correlation between repeated observations, and the reliability of the daughter's dam (bull's mate) information. Based on

the results of this simulation study, use of either the effective daughter contribution considering information of the daughter's dam (w_6) or the effective daughter contribution considering information of all female ancestors of the daughter (w_7) would improve international genetic comparisons. Both weighting factors yielded similar results, but w_6 is easier to compute than w_7 because it does not require accumulation of information on all female ancestors.

Weighting factors w_5 , w_6 , and w_7 were based on the concept of daughter equivalents (VanRaden and Wiggans, 1991) and, in this study, were derived for national evaluations based on single-trait (repeatability) animal models. Weighting factors for other classes of models can be derived on the basis of selection index methodology, as well as by using specific components of the mixed model equations.

Weighting factors w_5 , w_6 , and w_7 ignore the distribution of daughters of a sire across CG levels. They assume that two daughters in one group contribute the same amount of information as two daughters with records in different groups. Generally, the effect of this assumption is expected to be relatively small as can be seen from comparing w_2 and w_3 (Tables 2, 5, and 6). For certain bulls, such as herd/breeder proven bulls, however, ignoring this effect may severely overestimate the contribution of daughters to the breeding values. Adjusting the number of lactations by the ratio of number of contemporaries with different sire and CG size would overcome this problem. Such bulls, however, are usually being excluded from routine international genetic evaluations.

An alternative to computing new weighting factors would be to use reliabilities of national genetic evaluations in the context of international comparisons. Several methods have been proposed to compute effective number of daughters based on such reliabilities (George et al., 1994; Sullivan et al., 1998; VanRaden, 2000). However, a prerequisite for application of these methods to routine international genetic evaluation is that national reliabilities are computed in the same way in all countries. A small, informal survey revealed considerable differences in approximation methods for national reliabilities. Fikse and Sullivan (1999) showed in a simulation study that weighting factors based on national reliability are seriously affected by bias in such reliabilities and may introduce errors in international genetic evaluations.

International breeding values for bulls with national evaluations in one population were affected little by the choice of weighting factor. This happened partly because populations generated in this simulation were well connected. For bulls with daughters in only one population, the Mendelian sampling deviation in the

country of origin is converted and added to the pedigree index on the foreign scale. When genetic ties are weak, male ancestors generally have little information in the foreign country and the pedigree index in the foreign country is also based on a conversion. In such cases, the choice of weighting factor will have a large impact on international breeding values. In this study, MSEF on the foreign scale for bulls originating in the same population as their parents were more affected by the choice of weighting factor compared with bulls with parents from the other population (results not shown).

CONCLUSIONS

Using weighting factors that incorrectly assessed the precision of daughter information led to biased estimates of sire variance. International breeding values for bulls were affected little by the choice of weighting factor. However, the effect depends on the similarity of national genetic evaluations, and the variation in national genetic evaluations is larger than what was considered in this simulation study. The effect of the weighting factor used in this study on international reliabilities was considerable, especially when national genetic evaluations were based on multiple lactations.

Results from this simulation study suggest that weighting factors for sire daughter information in international genetic evaluations should consider contemporary group structure, the correlation between observations on the same animal, and the reliability of daughters' female ancestors. Among the seven weighting factors investigated, two weighting factors (w_6 and w_7) consider these effects, and these two performed similarly.

ACKNOWLEDGMENTS

The authors thank Didier Boichard, Les Jones, Pete Sullivan, and Paul VanRaden for feedback and fruitful discussions. Financial support was provided by a USDA/NAAB research grant.

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